

Short Communications

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Age and Sex Differences in Wing Loading and Other Aerodynamic Characteristics of Merlins

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ABSTRACT.—We examined age and sex differences in wing loading, aspect ratio, and wing span in a sample of 208 Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993. We also examined differences in tail loading of 166 of these Merlins. Adult males had significantly greater mass and wing loading than juvenile males. Adult females differed significantly from juvenile females only in mass. Females were significantly greater than males in every measure except aspect ratio. There were no apparent age differences in tail area or flight surface loading, but females had greater values in both. Merlins show fewer age differences in aerodynamic characteristics than Sharp-shinned Hawks (*Accipiter striatus*), probably because of differences in how the two species pursue and capture avian prey. Merlins usually capture prey in the air, sometimes after multiple stoops and at high flight speeds. In contrast, Sharp-shinned Hawks take birds from their perch or after a brief chase, often in dense vegetation, at relatively low flight speeds. Slower flight speeds require larger control surfaces and can explain the increased age differences in wing and tail areas in Sharp-shinned Hawks.

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Wing area, wing loading, and other aerodynamic characteristics are especially important for those diurnal birds of prey which spend considerable time on the wing and rely on agility in flight for the capture of prey. Adult Sharp-shinned Hawks (*Accipiter striatus*) have significantly greater wing lengths, wing widths, aspect ratios, wing areas, mass, and wing loadings than juveniles, and all of these measures are significantly greater in fe-

males than in males (Mueller et al. 1981). Brown and Amadon (1968) summarized the data on wing loading available for Falconiformes: measurements of wing loadings were available for only 56 species, half of these were represented by samples of only one, both sexes were measured for only seven species, and age was not noted for any. Since that time, data for both sexes have been published for only six species. Only one sample of wing loading for each sex was reported for the Ferruginous Hawk (*Buteo regalis*), the Red-tailed Hawk (*B. jamaicensis*), and the Swainson's Hawk (*B. swainsoni*; Janes 1985). Marsh and Storer (1981) reported wing loadings for 21 male and 24 female Cooper's Hawks (*A. cooperii*), and Jenkins (1995) provided wing loadings for 13 male and 20 female Peregrine Falcons (*Falco peregrinus*) and 20 male and 20 female Lanner Falcons (*F. biarmicus*). Age of the birds was not indicated in any of the three studies. Amadon (1980) compared the areas of juvenile and adult raptors (primarily wing and tail length) and found that in the smaller falcons (including the Merlin) juveniles "are smaller or about the same as the adult." This leads to a prediction that age differences in wing loading and other characteristics in Merlins would be less than that of Sharp-shinned Hawks. In this paper we examine age and sex differences in wing loading and other aerodynamic characteristics of Merlins (*F. columbarius*) based on a sample of 208 wings and 166 tails.

STUDY AREA AND METHODS

We captured Merlins during fall migration, 1978–1993, at the Cedar Grove Ornithological Station (43° 33' N, 87° 21' W) on the western shore of Lake Michigan in Sheboygan County, Wisconsin. The methods used to obtain the data are explained in detail in Mueller et al. (1981). Briefly, the extended wing (or tail) was held up against a vertical sheet of Plexiglas ruled into 5-cm squares and photographed. The negatives

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TABLE 1. Wing area, wing loading, and other characteristics of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993.

Measurements	Adult males (n = 57)		Juvenile males (n = 52)		Adult females (n = 49)		Juvenile females (n = 50)	
	mean	SD	mean	SD	mean	SD	mean	SD
Wing chord (cm)	19.3	0.40	19.1	0.52	21.3	0.40	21.2	0.38
Wing length (cm)	25.7	0.72	25.5	0.79	28.6	0.96	28.3	0.96
Wing width (cm)	7.5	0.33	7.6	0.29	8.5	0.32	8.5	0.42
Wing span (cm)	57.0	1.44	57.7	1.47	63.7	1.99	63.3	1.76
Aspect ratio	7.64	0.33	7.56	0.20	7.50	0.33	7.27	1.40
Wing area (cm ²)	425.9	22.42	441.2	21.81	542.6	33.60	537.9	46.65
Mass (g)	160.2	8.76	153.6	9.74	222.4	13.75	212.3	12.41
Wing load (g/cm ²)	0.373	0.03	0.348	0.02	0.405	0.03	0.400	0.04

later were projected to life size and an outline drawn of the wing (or tail). We measured the area of the drawing with a compensating polar planimeter. Measurements were taken as in Mueller et al. (1981) except for the following: (1) wing area was twice the area of one wing plus the area of the body adjacent to the wing, and (2) aspect ratio was the square of wing span divided by wing area. We aged the falcons by plumage (Sodhi et al. 1993) and we sexed juveniles by size. The mean wing chord of 618 juvenile Merlins sexed as males at Cedar Grove was 192.06 ± 3.56 SD and of 648 sexed as females was 212.63 ± 4.04 SD, indicating that >99% of the birds could be sexed correctly by wing chord alone. We performed statistical tests with SYSTAT (Wilkinson 1989) on a Macintosh G3 computer. We used *t*-tests for independent samples for all comparisons.

The tails of the falcons were spread to varying degrees and the areas varied accordingly. Estimates were necessary to standardize tail area. We used the following formula to estimate tail area:

$$\text{Area} = (A/360)(\pi B^2 - \pi C^2),$$

where A is the angle formed by lines drawn along the two outer rectrices until they meet on a drawing made from a photograph of the tail, B is the distance from the apex of this angle to the tip of the longest rectrix,

and C is B minus the tail length measured on the live bird. Unlike for Sharp-shinned Hawks (Mueller et al. 1981), this formula was a better fit than one using the sine of the angle and the length of the tail ($r = 0.95$ and $r = 0.89$, respectively). A folded tail of a Merlin probably is held at an angle of 10° and a spread of 110° probably is the maximum possible without gaps between the rectrices. Statistical tests of significance were not used to compare tail areas because those estimates were derived.

RESULTS AND DISCUSSION

Juvenile males had greater wing widths and wing areas than adult males, but neither difference was significant (Tables 1 and 2). Adult males had a greater wing chord, wing length, aspect ratio, mass, and wing loading than juvenile males, but only the last two differences were significant. Adult females were larger than juvenile females in all of the above measures, but only the difference in mass was significant. Females were considerably larger than males and differed significantly in every individual measurement. The sex difference in

TABLE 2. Age and sex comparisons of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993. Means and standard deviations are presented in Table 1.

Measurements	Age comparisons				Sex comparisons			
	Males (df = 107)		Females (df = 97)		Adults (df = 104)		Juveniles (df = 101)	
	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Wing chord	1.43	0.16	0.31	0.19	26.40	0.00	23.26	0.00
Wing length	1.68	0.10	1.60	0.11	17.39	0.00	25.48	0.00
Wing width	1.53	0.13	0.75	0.45	16.05	0.00	11.58	0.00
Wing span	1.98	0.05	0.23	0.82	19.20	0.00	14.79	0.00
Aspect ratio	2.77	0.08	0.25	0.81	2.35	0.03	0.23	0.82
Wing area	0.23	0.82	1.25	0.22	21.47	0.00	14.98	0.00
Mass	3.71	0.00	3.68	0.00	28.47	0.00	26.74	0.00
Wing load	2.92	0.00	1.62	0.11	6.61	0.00	7.00	0.00

TABLE 3. Estimated tail area of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration 1978–1993.

	n	Tail length (cm)	Area (cm ²) at angle of spread	
			10°	110°
Adult male	49	11.5	27.6	180.0
Juvenile male	43	11.6	27.8	181.6
Adult female	44	12.9	35.7	216.8
Juvenile female	45	12.9	35.6	215.5

wing loading was highly significant in both adults and juveniles, but the difference in aspect ratio was significant only in adults. Females had larger tail areas than males (Table 3). Females also had greater surface loadings than males (Table 4), but there were only slight differences between juveniles and adults.

Mueller et al. (1981) found that adult Sharp-shinned Hawks had significantly shorter tails, longer and wider wings, greater wing areas, higher wing loadings, and higher aspect ratios than juveniles. They hypothesized that adults flew faster and struck prey more forcibly, but required more energy consumption than juveniles. They proposed that juveniles were more maneuverable and required less energy in flight than adults and that this was an adaptation for the juveniles until they developed hunting skills for adult life. The pattern we found in Merlins is partially in agreement with this hypothesis. Adult males had greater wing loading and mass than juvenile males; however, the only significant age difference in females was in mass.

Sharp-shinned Hawks exhibit much greater age differences in aerodynamic characteristics than Merlins. Both species feed primarily on birds and have similar fledgling dependency periods (Sodhi et al. 1993, Bildstein and Meyer 2000). The major difference between the species is in how they hunt and capture birds. Sharp-shinned Hawks capture perched birds, often in dense vegetation, or in flight after a brief chase. Merlins usually capture birds in the air, often after a series of stoops at a flight speed considerably greater than that of Sharp-shinned Hawks. The tail and wings are used to deflect the airstream in rapid twists and turns. The force produced by such a deflecting surface is proportional to the area of the sur-

TABLE 4. Flight surface area (wing plus tail at 110° angle of spread) and flight surface load (mass/flight surface area) of Merlins (*Falco columbarius*) captured at Cedar Grove, Wisconsin, during fall migration, 1978–1993.

	n	Flight surface (cm ²)	Flight load (g/cm ²)
Adult male	49	605.9	0.264
Juvenile male	43	622.8	0.247
Adult female	44	759.4	0.293
Juvenile female	45	753.4	0.282

face and the square of the airspeed, so a falcon in rapid flight needs less deflecting surface than a hawk in slower twists and turns. The tail of birds functions primarily as a control surface and a decrease in the ratio of mass to tail surface at maximum spread would increase maneuverability. This ratio in Sharp-shinned Hawks is only 58% of that of Merlins, suggesting that the former is considerably more maneuverable than the latter at equal airspeeds. The smaller age differences in wing width, wing length, and wing loading in Merlins, compared to Sharp-shinned Hawks, also can be attributed to Merlins not requiring relatively large control surfaces. Perhaps young Sharp-shinned Hawks need the additional maneuverability and economy in flight offered by lower flight loading, shorter wings, and longer tails, but these are of no advantage to young Merlins because speed is of prime importance in the pursuit of their prey.

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Social and Breeding Biology of Bee-eaters in Thailand

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ABSTRACT.—I report on the social and breeding biology of four bee-eater species in Thailand. Little Green Bee-eaters (*Merops orientalis*) breed cooperatively in clusters of overlapping territories. Cooperative breeding units have one to two helpers that join the breeding pair only after incubation has begun. Nests rarely are left unguarded due to threats of predation and possible intraspecific brood parasitism. Males also guard their mates against extrapair copulations. The Blue-tailed Bee-eater (*M. philippinus*) breeds cooperatively and has a complex social system, with evidence suggestive of intraspecific brood parasitism and extrapair copulation. I provide evidence that the Bay-headed Bee-eater (*M. leschenaulti*) breeds cooperatively and report observations of noncooperative breeding at one nest in the Blue-bearded Bee-eater (*Nyctyornis athertoni*).

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The bee-eaters (Aves: Meropidae) are a clade of 26 species with considerable diversity in social and breeding behaviors. This behavioral diversity includes colonial and solitary nesting, migratory and sedentary populations, and cooperative and noncooperative breeding systems. However, for several species data on these behaviors are lacking. These data are crucial for comparative studies concerning the

evolution of, and the ecological influences on, bee-eater social system diversity. This paper describes aspects of the social structure and breeding biology of four bee-eater species breeding in Thailand.

The Little Green Bee-eater (*Merops orientalis*) is the most variable species in the family in regard to plumage color and can be subdivided into 6–8 geographically variable races (Fry 1984). Whether this species also shows variation in social and breeding behaviors in populations ranging from western sub-Saharan Africa through the Middle East and Indian subcontinent to south Asia is not known. To address this question, I compare the social system of Little Green Bee-eaters that were studied in Thailand and in India (Sridhar and Karanth 1993). Little information previously was available on the breeding biology of the Blue-tailed Bee-eater (*M. philippinus*), except that it sometimes nests in colonies (Fry et al. 1992). Here I show that this species breeds cooperatively and has a complex social system similar to other colonial bee-eaters. Lastly, I briefly describe the social system of the Bay-headed Bee-eater (*M. leschenaulti*) and the Blue-bearded Bee-eater (*Nyctyornis athertoni*).

METHODS

I made behavioral observations from 12 March through 5 May 1996. I studied Little Green Bee-eaters at Khao Sam Roi Yot National Park (99° 55' E, 12°

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